Biology of *Lespesia archippivora* (Diptera: Tachinidae)[1]

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The present study is concerned with the biology of *Lespesia archippivora* (Riley), a tachinid parasite of the monarch butterfly, *Danaus plexippus* (L.). This tachinid was purposely introduced from North America into the Hawaiian islands, probably from California (Fullaway, 1945; Pemberton, 1948), by Albert Koebele about 1898 for the control of armyworms (Swezey, 1923, 1927). At present it is widely distributed in the Hawaiian islands where it is frequently found in the lowlands (Bryan, 1923, 1926, 1933; Fullaway, 1945). In 1926 Bryan found a single specimen on Nihoa island.

The number of insects known to be parasitized by *L. archippivora* comprises 25 species of Lepidoptera and one Hymenoptera (Beneway, 1963). In the Hawaiian Islands the insects parasitized by *L. archippivora* include the monarch butterfly, *D. plexippus* (L.); armyworm, *Pseudoletia unipuncta* (Haworth); cabbage butterfly, *Pieris rapae* (L.); sugarcane leaf roller, *Hedylepta accepta* (Butler); painted lady, *Vanessa cardui* (L.); corn earworm, *Heliothis zea* (Boddie); black cutworm, *Agrotis ypsilon* (Rottemburg); and coconut leaf roller, *Hedylepta blackburni* (Butler).

MATERIALS AND METHODS

Laboratory studies were carried out at the University of Hawaii. Laboratory temperature ranged from 20.0°C to 32.5°C with a mean of 26.3°C. Relative humidity ranged from 47.5 to 71 percent with a mean of 59.3.

Rearing of Host. The host was reared on crown flower, *Calotropis gigantea* (L.) Robert Brown, leaves as described by Etchegaray and Nishida (1974).

Rearing of Parasite. Culture of *L. archippivora* was initiated with individuals that emerged from field collected *D. plexippus*. The hosts were collected in the larval stage from *C. gigantea* and reared in the laboratory until *L. archippivora* emerged. When the adult parasites emerged they

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were placed in a cage, 70 cm x 45 cm x 55 cm. The flies were fed sugar cubes and dry hydrolyzed protein. Water was also supplied.

Longevity Studies. For longevity studies newly emerged adults were immobilized by exposing them to -3°C for 5 to 10 minutes, sexed under a dissecting microscope and marked on the thorax with tempera colors to identify each individual. The flies of both sexes were then released in cylindrical cages, 46 cm high and 45 cm diameter. The flies were fed as mentioned above. Daily observations were made and the number of dead flies recorded.

Fecundity Studies. Parasites were allowed to oviposit on the larvae of *D. plexippus* by placing each mated female individually in a jar, 16 cm high and 6 cm in diameter. The host larva was then placed on a piece of *C. gigantea* leaf, and while holding the leaf with forceps, the inverted jar containing the parasite was placed over the leaf. The parasite usually began ovipositing on the caterpillar within a few minutes. The number of eggs laid on each caterpillar was then counted under a dissecting microscope. The procedure was repeated every day until the female died. After death the female was dissected and the eggs remaining in the uterus were counted.

Data on potential fecundity were obtained on ten mated females that had not yet oviposited. The reproductive system of these females, which were 6 to 8 days old, was dissected in Ringer's saline solution and the uterine eggs were counted.

Results

Immature Stages. The eggs were laid on the integument. After eclosion the first-instar larva bored into the host body with the transparent chorion still attached to the host integument. When the host was dissected the larva was observed moving freely within the body cavity. Three days after entry it attached itself near a spiracle of the host and became surrounded by host tracheae. At this time the respiratory funnel developed. The funnel of this species is of host tracheal origin similar to that described by Clausen (1940). The first-instar larva appeared to have no preference as to the site of attachment to the trachea. Moulting took place within the respiratory funnel.

The location of the second-instar larva within the host was the same as that of the first instar. During this stage the anterior portion of the body projected out of the tracheal funnel and the segmentation of the body was conspicuous. When disturbed with a needle the larva came out of the funnel.

In the third instar, the funnel covered only the posterior half of the body so that the larva was able to move the free anterior part back and forth within the body cavity of the host. The third-instar larva, being a voracious feeder, consumed the internal contents of the host almost completely, leaving only the host cuticle. The entire feeding process was

accomplished while its posterior end remained attached to the respiratory funnel.

When full grown the larva of the parasite emerged from the host and pupated. It was observed that the third-instar larva of *L. archippivora* always emerged from the fifth-instar larva of *D. plexippus* in the laboratory. However, with parasitized larvae collected from the field the parasites usually emerged from pupae.

Growth Rate. Growth rate was determined by measuring the length of the mouth hooks of the three instars. The data obtained indicated a linear relationship between the natural log of the length of mouth hooks and instars (Fig. 1). The regression equation is $Y = 0.9694X - 2.9507$.

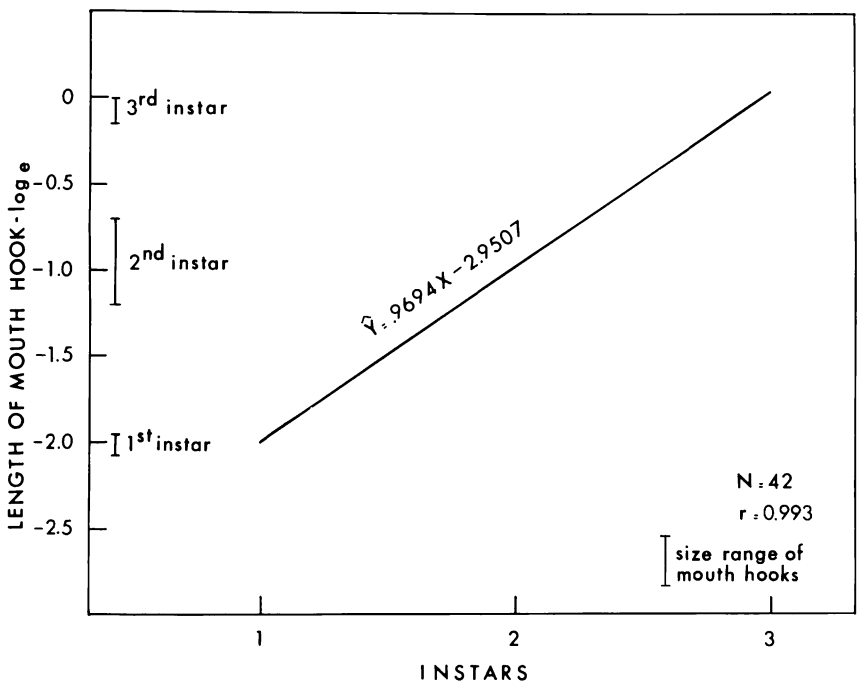

FIG. 1. Increase in length of mouth hooks in relation to the development of the larval stage of *L. archippivora*.

Effect of Age of Host on Parasitism. The number of instars of the parasite and the duration of each were determined by dissecting the larvae of *D. plexippus* at different intervals after exposure to the fly. The host larvae were killed in hot water and then placed in a petri dish with a layer of wax on the bottom. The head and last segment of the body were pinned and the dorsal skin was cut longitudinally using micro-dissecting scissors. The skin was carefully opened and pinned. After the maggots were

located they were removed with a fine-point dropper and killed in KAAD larval fixative solution. The time the larvae were kept in KAAD varied with the size of the larva, approximately 2-3 minutes for the smallest and 10 minutes for the largest.

TABLE 1.—*Mean Duration of Larval Instars of* L. archippivora *when Reared on Larvae of Different Ages of* D. plexippus

Instar of host	Number of host larvae exposed	Mean duration (days)	Range (days)	Standard Deviation (days)
1	4	15.2	15-16	0.50
2	4	18.7	16-24	3.80
3	13	15.8	12-20	2.15
4	93	11.3	8-14	1.42
5	1	7.0	.....	.....

The total duration of parasite larval stage when parasitization is initiated in the various instars of *D. plexippus* is shown in Table 1. Only one fifth instar *D. plexippus* was successfully parasitized in this experiment. Parasites usually were unable to parasitize fifth-instar larvae because these were able to shake flies off their body by vigorous movement of the head.

The mean duration of the larval stage of *L. archippivora* when eggs were deposited on first-instar larvae of *D. plexippus* was 15.2 days and 18.7 when deposited in the second instar.

Host Reaction to Parasite. The host larvae reacted in different ways when the parasite attempted to oviposit on its body. It was observed that the host moved the anterior part of the body up and down, and also from side to side when the parasite went near it. At the time of attack the larva exuded a copious amount of green liquid, presumably through the integument, and the liquid was observed on the body as well as on the leaf on which the larva was present. No reference was found in the literature on this exudation. Its function is perhaps defense against attack. It is also possible that the exuded material made it difficult for the adhesion of the egg to the integument, but it seemed that it did not kill the parasite egg.

Many larvae rolled their bodies into a ball. When already parasitized some caterpillars released a transparent liquid through the mouth. Another common reaction in parasitized larvae was the bending of the body back posteriorly and moving the mouth as though they were trying to remove the eggs.

Number of Parasites Per Host. Data on the number of parasites per host were based on the number of larvae that emerged from field collected hosts. The frequency distribution of the number of parasites that emerged per host, shown in Table 2, indicates that the number of parasites per

TABLE 2.—*Observed and Expected Number of Parasites per Larva of* D. plexippus

Number of parasites per host	Observed Frequency	Expected Frequency	Chi-Square	Probability[1]
1	34	22	6.5454	*
2	16	26	3.8461	*
3	16	21	1.1904	N. S.
4	13	12	0.0833	N. S.
5	5	6	0.1666	N. S.
6	2	2	0.0000	N. S.
7-10	4	1	8.2880	**
			Total 20.1198	

[1] Calculated by the method of Cohen (1960); * = significant, ** = highly significant.

host ranged from 1 to 10 with the highest frequency being 1 parasite per host.

To test whether parasites were randomly distributed with respect to hosts the data were fitted to a truncated Poisson distribution using the method of Cohen (1960). The chi-square test gave a total chi-square value of 20.119 (df = 5) and the probability was less than 0.01. Therefore, the data did not fit a truncated Poisson distribution. The classes 1, 2 and 7-10 were significantly different (Table 2). From this it was concluded that the parasites were not randomly distributed among the hosts.

Adult Behavior. Copulation occurred usually within 24 hours after emergence. During copulation the female remained motionless while the male affixed itself on the dorsal part of the female. With its fore, middle and hind legs the male grasped the thorax, wings and posterior part of the female respectively. The duration of mating was 5 to 15 minutes. The oviposition behavior of *L. archippivora* was observed in the laboratory. When a female was ready to lay eggs it became very active in the vicinity of the host, walking and flying continuously. Prior to oviposition the parasite projected the ovipositor outward and rubbed it with the posterior legs. It also rubbed the posterior legs against one another many times. The assault by the parasite was very sudden. Usually the parasite attacked from the posterior end of the host, grasping it with the fore legs and at the same time bending the tip of the abdomen under and forward between the legs. Although the attack occurred from the posterior end of the host, the parasite often turned towards the side and laid eggs on the side of the body. After ovipositing the female remained near the host, rubbing the wings with the legs for varying periods of time before resuming the attack. The fly sometimes went through all the motions of oviposition, but did not lay any eggs. The parasite attacked all larval stages of *D. plexippus,* but showed a preference for the late second-, third- and early fourth-instar larvae. It was unusual for the fly to lay eggs on first-instar larvae.

Superparasitism was commonly observed in the laboratory. When excessive numbers of eggs (as many as 20) were deposited on one caterpillar it usually died before completion of the development of the parasites.

The distribution of eggs by this tachinid was determined by noting the location of eggs on the bodies of 24 caterpillars. Eggs laid on the intersegmental membranes were considered as laid on the preceding segment, e.g.: eggs laid between segment 1 and 2 were counted as those laid on segment 1. Figure 2 shows that the number of eggs laid on the right

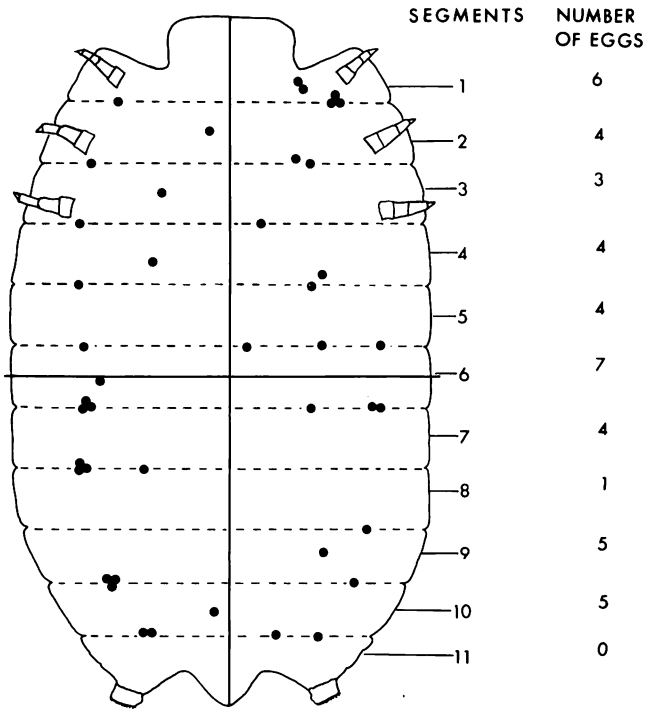

FIG. 2. Diagrammatic presentation of the distribution of eggs of *L. archippivora* on 24 larval skins of *D. plexippus*. The number of parasites eggs per larva ranged from 1 to 5.

and left sides were about the same, 22 on the left side and 21 on the right side. A chi-square test was applied to the number of eggs laid per segment on the left and right sides. Although it was recognized that small numbers were involved, the test showed that there was a significant difference only on segment 7; all the other segments showed no significant difference in the number of eggs laid on the left and right sides. Figure 2 also shows that there is no significant difference in the number of eggs laid on the anterior and posterior portions of the body; 21 and 22 eggs respectively. However, in regards to the number of eggs laid per segment on the entire

body, it was found that the egg distribution was not equal on all segments but was highest on segments 1 and 6.

Fecundity. The actual and potential fecundity of *L. archippivora* were determined. To determine actual fecundity, nine females were allowed to lay eggs throughout their life span and the number of eggs laid recorded. After death the eggs remaining in their reproductive systems were counted. The number of eggs laid per female during the entire life span ranged from 15 to 204 with a mean and standard deviation of 105.8 ± 53.6. The total number of eggs that these females might have been able to lay, taking into consideration those eggs that remained in the reproductive system after death, ranged from 82 to 206 with a mean of 142.5 ± 40.1.

The potential fecundity was determined by dissecting the reproductive system of ten mated females that had not yet oviposited. The number of eggs found in their uteri ranged from 135 to 291 with a mean of 202.6 ± 58.7. A t-test of significance applied to these data showed a significant difference between actual and potential fecundity ($t = 2.57$; $df = 17$; $P < 0.05$).

Sex Ratio and Longevity. Data on sex ratio of *L. archippivora* were obtained from 208 adults reared in the laboratory. Of these 116 were males and 92 females. The data were subjected to a chi-square test, with correction for continuity and on the hypothesis that the sex ratio was 1:1. The computed chi-square value of 2.542 ($P > 0.05$) was consistent with the hypothesis.

Data on longevity of *L. archippivora* were obtained from 60 individuals, 36 males and 24 females. Under laboratory conditions longevity of males ranged from 3 to 39 days with a mean of 16.3 ± 11.3 days, and that of females was 3 to 46 days with a mean of 22.2 ± 14.5 days. The t-test of significance indicated no significant difference between the longevity of males and females ($t = 0.563$; $df = 57$; $P > 0.05$).

Life Table of L. archippivora. The survival of *L. archippivora* in the laboratory was studied by means of a life table (Table 3). The notations

TABLE 3.—*Life Table of* L. archippivora *when Reared on* D. plexippus *larvae*

x	lx	dx	100 qx	100 rx
Age interval	No. alive at beginning of x	No. dying during x	dx as percentage of lx	dx as percentage of original no. of eggs
Egg	514	398	77.4%	77.4%
Larvae (third instar)	116	0	0.0%	0.0%
Pupa	116	16	13.7%	3.1%
Adult	100	1*	1.0%	0.1%
Female	41			
Male	59			

*Wing deformed.

of the columns of the life table are in accordance with those of Morris and Miller (1954). Column dxF, (factor responsible for mortality of the corresponding developmental stage) has been omitted in this analysis. The life table was made using eggs, third instar larvae, pupae and adults. Other larval stages were not included because, being within the host, it was difficult to obtain survival and mortality data. The life table study began with 514 eggs of *L. archippivora* that were laid on larvae of different instars of *D. plexippus*. From these only 116 reached third instar and 398 individuals (77.4%) died. All third-instar larvae pupated. Out of the 116 pupae 100 adults were obtained, and the remaining 16 pupae (13.7%) died in the pupal stage. Of the original 514 eggs, 80.5% died before reaching adult stage.

Discussion

Third-instar larvae of *L. archippivora* in the laboratory always emerged from the fifth-instar larvae of *D. plexippus,* while those collected from the field usually emerged from the pupal stage. One possible explanation for this difference is that in the field older larvae were parasitized and thus the parasites did not reach full development until hosts were in the pupal stage. Although there are no data, a second possible explanation is that under laboratory conditions larvae may have grown more slowly than unconfined larvae, with the result that parasite development was completed at an earlier stage of host development.

Data on potential fecundity obtained in the present study were significantly higher than actual fecundity. The latter may have been underestimated because in the difficulty in counting all eggs laid on the caterpillars. Furthermore, some eggs could have fallen off the hosts. The potential fecundity appeared to be a better measure of fecundity than actual fecundity.

Fecundity of *L. archippivora* was also measured by Bryan et al. (1969) by counting the number of puparia produced from *Spodoptera exigua* (Hubner) larvae. They found that the number of offspring changed with temperature and the number of hours each female oviposited per day. Their data were difficult to compare with those obtained in the present study because of the different host and methods used. It should be mentioned, however, that the maggot production in the present study was about 20% of the real fecundity. If we assume this relationship for the parasite in Arizona, then its fecundity would have been higher than that of the Hawaiian parasite.

Summary

There was a linear relationship between the natural log of the length of mouth hooks of *Lespesia archippivora* and instars. The number of parasites per *Danaus plexippus* larva ranged from 1 to 10 with the highest frequency at 1 parasite per host; the parasites were not randomly

distributed among the hosts. Copulation of *L. archippivora* occurred usually within 24 hours after adult emergence. The average number of eggs laid per female of *L. archippivora* was 105.8±53.6. The fecundity determined by dissection of ten mated females that had not oviposited was 202.6±58.7. The survival of *L. archippivora* was determined in the laboratory by means of a life table.

LITERATURE CITED

Beneway, D. F. 1963. A Revision of the Flies of the Genus *Lespesia (= Achaetoneura)* in North America (Diptera: Tachinidae). Univ. Kansas Sci. Bull. **44(13)**: 627-677.

Bryan, E. H. 1923. Insects from the Summit of Mauna Kea. Proc. Hawaii. Entomol. Soc. **5(2)**: 287-288.

Bryan, E. H. 1926. Additional Notes on the Insects Occurring on Mauna Kea and Mauna Loa. Proc. Hawaii. Entomol. Soc. **6(2)**: 280-282.

Bryan, E. H. 1933. A Review of the Hawaiian Diptera, with Descriptions of New Species. Proc. Hawaii. Entomol. Soc. **8(2)**: 399-468.

Bryan, D. E., C. G. Jackson and R. Patana. 1969. Effect of Temperature on the Progeny Production and Longevity of *Lespesia archippivora* in the Laboratory. J. Econ. Entomol. **62(4)**: 765-767.

Clausen, C. P. 1940. Entomophagous Insects. Hafner Publishing Company. New York. 688 pp.

Cohen, A. C., Jr. 1960. Estimating the Parameter in a Conditional Poisson Distribution. Biometrics. **16(2)**: 203-211.

Etchegaray, J. B. and T. Nishida. 1973. Reproductive Activity, Seasonal Abundance and Parasitism of the Monarch Butterfly, *D. plexippus* (Lepidoptera: Danaidae) in Hawaii. Proc. Hawaii. Entomol. Soc. **21(3)**: 33-39.

Fullaway, D. T. and N. L. H. Krauss. 1945. Common Insects of Hawaii. Tongg Publ. Co., Honolulu, Hawaii. 228 pp.

Morris, R. F. and C. A. Miller. 1954. The Development of Life Tables for the Spruce Budworm. Canadian J. Zool. **32(4)**: 283-301.

Pemberton, C. E. 1948. The Control of Grass Armyworm, *Laphygma exempta* (Walker), in Hawaii by Parasites. Hawaiian Planter's Record. **52**: 181-200.

Swezey, O. H. 1923. Records of Introduction of Beneficial Insects into the Hawaiian Islands. Proc. Hawaii. Entomol. Soc. **5(2)**: 299-304.

Swezey, O. H. 1927. Notes on the Mexican Tachinid, *Archytas cirphis* Curran, Introduced into Hawaii as an Armyworm Parasite (Diptera). Proc. Hawaii. Entomol. Soc. **6(3)**: 499-503.